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New Genetic and Linguistic Analyses Show Ancient Human Influence on Baobab Evolution and Distribution in Australia

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Abstract

This study investigates the role of human agency in the gene flow and geographical distribution of the Australian ba
Adansonia gregorii. The genus *Adansonia* is a charismatic tree endemic to Africa, Madagascar, and northwest Aust
long been valued by humans for its multiple uses. The distribution of genetic variation in baobabs in Africa has beer
attributed to human-mediated dispersal over millennia, but this relationship has never been investigated for the Aus
We combined genetic and linguistic data to analyse geographic patterns of gene flow and movement of word-forms
the Aboriginal languages of northwest Australia. Comprehensive assessment of genetic diversity showed weak geo
structure and high gene flow. Of potential dispersal vectors, humans were identified as most likely to have enabled
across biogeographic barriers in northwest Australia. Genetic-linguistic analysis demonstrated congruence of gene
and directional movement of Aboriginal loanwords for *A*. *gregorii*. These findings, along with previous archaeobotar
from the Late Pleistocene and Holocene, suggest that ancient humans significantly influenced the geographic distri
Adansonia in northwest Australia.

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Introduction

The role of humans in shaping crop genetic diversity has always been considered an integral factor in the evolution
various regions of the world [1–3]. Interdisciplinary research combining genetics, linguistics, and archaeobotany ha
enhanced understanding of the geographic patterns of animal and crop domestication and subsequent diffusion by
Yet, there is very little comparable research on how anthropogenic agency has influenced the evolution and distribu
uncultivated plants that, nonetheless, have a long history of human use [4–6]. A striking example is that of *Adansor*
tree, an iconic genus endemic to Africa, Madagascar, and the Kimberley region of northwest Australia [7,8]. These
trees hold significant cultural symbolism and multipurpose value as sources of food, medicine, water storage, shelte
material for artisanal products in all these places [9–17]. Although there is no evidence of baobabs being cultivated
distribution of the African baobab species, *Adansonia digitata* L., has been closely linked to human dispersal and se
patterns [18,19]. This association is also recognised by the diversity and borrowing of terms for baobabs between la
in Africa [4, 16]. In contrast, previous research on the evolution and geographic distribution of the Australian baobal
gregorii F. Muell., has been based on the assumption of long-term natural processes [7,8] without any significant int
human agency. This assumption may have stemmed from the long-held view of Aboriginal Australia as a ‘continent

gatherers' [20–24] where anthropogenic agency was limited to 'fire-stick farming' of landscapes for nomadic foragin [25,26]. We explore the role of humans in shaping the evolution of *A*. *gregorii* by determining whether the geograph genetic diversity is explained, in part, by patterns of human migration, as inferred from linguistic analysis.

Levels of genetic divergence show that *A*. *gregorii* separated from other *Adansonia* species more recently than the Gondwana, but before the arrival of humans in Australia [7,8]. Leong-Pock Tsy et al. [27] demonstrated that *A*. *digit* their viability in seawater, making oceanic current dispersal feasible. From this it can be inferred that *A*. *gregorii* has Australia for longer than humans. There is also the possibility, albeit a less parsimonious explanation, that the spec recently from an unknown population which is now extinct. One hypothesis outlining how *A*. *gregorii* may have arriv with humans has been explored in more detail by Pettigrew [28].

Adansonia gregorii, known in Australia as 'boab', is mainly distributed across the Kimberley region of northwest Aus small extension eastward into the Victoria River District in the Northern Territory. The distribution of *A*. *gregorii* in the extends from the northern coastline to the edge of the Great Sandy Desert and the Tanami Desert [17,29–32]. The region represents the westernmost extent of the Australian Monsoon Tropics (AMT), which is characterised by high rainfall and savanna vegetation [17,33]. The tree has been introduced more recently in urban centers of northern A ornamental purposes [17].

The AMT biome is bounded to the south by arid habitats, which began developing in the Late Cenozoic and contain different biota [34,35]. The major biogeographical divide in northwest Australia is between the Kimberley to the wes Land to the east, with more localized and specific barriers created by major river drainage systems [36–39]. Within phylogeographic patterns for rock-wallabies (*Petrogale* spp.) and other species suggest an East-West Divide runnin Central Kimberley [34,37,39]. Despite evidence of biogeographic barriers, a previously detailed population genetic *gregorii* has demonstrated that there is little genetic structure, with F_{ST} values non-significant between most popula geographic structure could be explained by a relatively recent arrival in the Kimberley, a recent genetic bottleneck, rates across the species' range. For reasons detailed in Bell et al. [40], high dispersal is the most likely explanation

In this paper we sought to evaluate the latter hypothesis – that the low levels of genetic structure within *A*. *gregorii* levels of gene flow and, specifically, that human-mediated seed dispersal has been an important evolutionary factor this species. Pollination in *A*. *gregorii* might occasionally entail birds or bats, but it appears that hawkmoths are the agents [17,29,33,41,42]. Pollination-mediated gene flow is limited to the paternal genome and, in insect pollinated s a less effective mechanism of long-distance gene flow than fruit dispersal [43–45]. Floodwaters could explain some [7,16], but would probably not spread seeds beyond the edges of seasonal waterways and alluvial flats due to the f dehiscent nature of the *A*. *gregorii* pericarp [7,33]. Other seed dispersing agents could be mammals such as rock w (*Petrogale* spp.), other wallabies and kangaroos (*Macropus* spp.), which eat the fruit and disperse the seeds in thei However, phylogeographic studies of the short-eared rock-wallaby (*P*. *brachyotis*), showed strong genetic structure at least this species has limited dispersal ability across biogeographic barriers in the Kimberley [39,46].

Anthropogenic agency has not been formally considered as a gene flow vector for *A*. *gregorii*, despite archaeologic long-term use by Aboriginal groups in the region [28,47–50]. This omission may be due to the fact that the boab wa historically, or not considered part of the food crops traditionally harvested by Aboriginal groups. Also, the presence pod remains at one or two archaeological sites is not sufficient to demonstrate anthropogenic dispersal across the geographic range. Additional evidence is needed to evaluate whether humans have played a role in boab gene flow that historical linguistics, which has been used in combination with other sources of data to trace geographic patter domesticated species [1–3], could be applied to a non-domesticated tree species such as *A*. *gregorii* [6]. Specificall we investigate the role of human agency in the gene flow of *A*. *gregorii* by testing for congruence between the spati genetic variation in *A*. *gregorii* trees and associated word-forms in the Aboriginal languages of northwest Australia. a high level of spatial overlap between the genetic and linguistic data. Our results indicate that, as previously shown in Africa [19,51,52], ancient humans have influenced the distribution of genetic diversity of *A*. *gregorii* in northern Au by acting as seed dispersal agents over long distances.

Materials and Methods

This study makes use of two recently published data sets relating to *A*. *gregorii* from different fields of research. The genetic data from six nuclear microsatellite loci, of 220 *A*. *gregorii* individuals [40] (S1 Dataset). Although the numbe microsatellite loci is low and can render some quantitative methods inaccurate, we used this data to make qualitativ on patterns of dispersal and relationship between populations. The second data set consists of the words used for Aboriginal languages from across the species range [53] (S2 Dataset). This study brings these two datasets togeth them simultaneously to detect any congruent patterns.

Phylogenetic analysis of microsatellite data

We conducted phylogenetic analysis of the *A*. *gregorii* populations shown in Fig. 1, using previously obtained micro [40]. Collection of plant material, with appropriate permissions, deposition of specimens, and laboratory analyses a Bell et al. [40]. This study used the spatial principal components analysis (sPCA) to map and define genetic popula identified five genetically differentiated clusters: West Kimberley (WK); East Kimberley (EK); North West Coast (NW (NC), and North East Coast (NEC). Genetic divergence between these clusters was weak, but statistically significa these were treated as five populations for subsequent analyses.

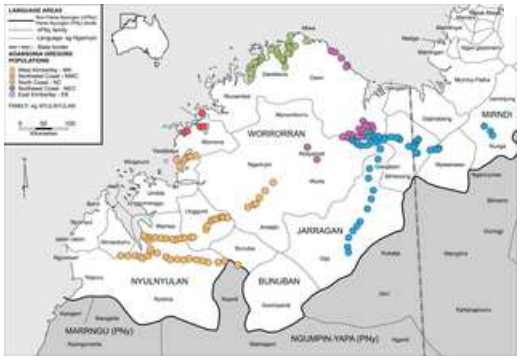

Fig 1. Graphical representation of the five inferred *Adansonia gregorii* populations from the sPCA, shown on a map of Aborigina areas of the Kimberley region.
Map based on Harvey [58] and McGregor and Rumsey [63].
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To obtain an estimate of the relationships among the five populations, we first obtained 1000 bootstrap replicates of microsatellite data. We calculated pairwise genetic distances between populations with the D_C method [54] for each replicate in Phylip v 3.69 [55]. These distance matrices were then used to construct unrooted neighbour-joining tree bootstrap consensus tree in Phylip. While more complex methods have been found to provide greater accuracy in d divergence events from microsatellite data, the simple D_C method was judged suitable because it performs as well methods at phylogenetic reconstruction [56]. The resulting tree was midpoint rooted.

Phylogeny of linguistic data

The Aboriginal languages of Australia are broadly classified into a number of families, Pama-Nyungan (***PNy***) and te non-Pama-Nyungan (***nPNy***) families [57,58]. The ***PNy*** language groups are most widespread across the continent, families (excluding Tasmania) exist primarily in northwest Australia across the Kimberley and western Arnhem Lanc ***PNy*** language subgroups and ***nPNy*** families have been distinguished by the comparative method [60], including gr morphology and measures of difference in vocabulary [57], with sub-groups identified by sets of 'shared innovations Neighbour Joining analysis of twenty-one Kimberley languages using the method described in Hudson and Bryant published by McGregor and Rumsey [63]. The tree generated from that analysis showed the relationships between languages based on lexical resemblances from a basic wordlist of 105 meanings, containing minimum numbers of A greater degree of proximity and shared branches in the phylogeny indicates higher lexical similarity between the languages. We used this neighbour-joining tree in conjunction with a more general consensus about family classific comparative method in discussion of the origins of words for the boab tree [64].

Determining boab proto-words, inherited forms, and loanwords

Data on boab word-forms and related terminology was drawn from both published and unpublished sources and tra a standard orthography [53] (S2 Dataset). The distinction between inheritance (vertical transmission) and borrowing transmission) of word-forms is vital to our analysis. Proto-words are word-forms that can be traced back through su plausible steps to a common ancestral word-form in an ancestral language (known as the proto-language) [60]. In v transmission, proto-words are inherited through nodes in a phylogeny to a number of more recent descendant lang changing meaning and form over time. Horizontal transmission, or diffusion, occurs through borrowing, whereby wo become adopted in other languages that may or may not be closely related by inheritance. There are several types used to detect loanwords and their original source [6]. Borrowed words in a language are ones that cannot be conn plausible proto-words in that language but instead show strong similarity to words in another language. The identifi loanword is further corroborated when the word can be analyzed into meaningful word-parts in the other language loan source) but not in a language into which it has been borrowed.

Genetic-Linguistic Analysis

The spatial distribution of each language was defined following Harvey [58] and McGregor and Rumsey [63]. The *A* distribution includes five ***nPNy*** families (Worrorran, Nyulnyulan, Bunuban, Jarragan, and Mirndi) and two ***PNy*** langu (Marrngu and Ngumpin-Yapa) (Fig. 1). Three sets of relationships of genetic and linguistic data for *A*. *gregorii* were evidence of human-mediated dispersal across the plant's geographic range.

Boab populations and language families.

Geographic congruence between *A*. *gregorii* populations and language areas was examined by superimposing the the phylogenetic tree of the main Kimberley language groups analysed by McGregor and Rumsey [63], and conver superimposing the language group areas [58] in which the boab populations occur on the neighbour-joining tree of populations (Fig. 2A and B). A high level of geographic congruence between the *A*. *gregorii* genetic populations an areas they occupy would be consistent with the idea that people have moved boabs extensively within language ar much between language areas.

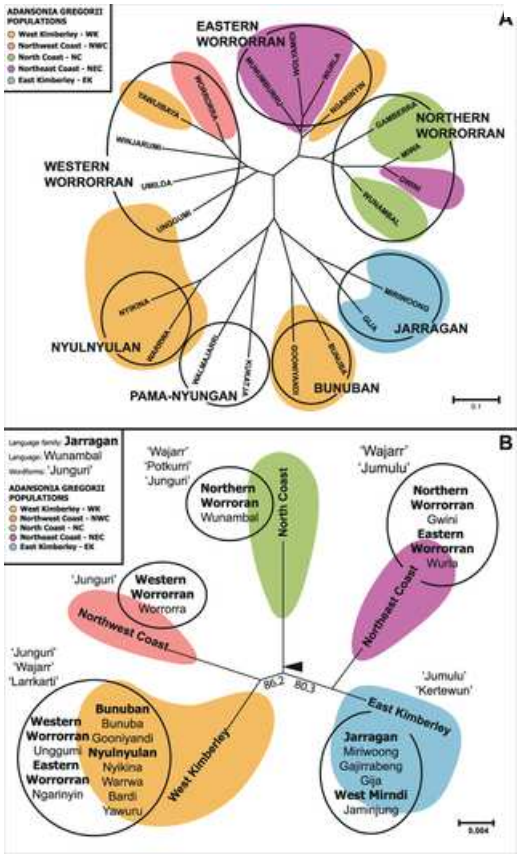

Fig 2. A. Neighbour-joining tree of lexical resemblance among Worrorran and nearby Aboriginal languages of the Kimberley, foll McGregor and Rumsey [63].

Twenty-one languages (19 belonging to ***nPNy*** families and 2 belonging to the Ngumpin ***PNy*** sub-group) were ch analysis on the basis of availability of relatively reliable information. Distance between nodes indicates degree of between the languages according to the scale shown. The five inferred *A*. *gregorii* populations have been superi the tree to visualize spatial congruence with language groups. **B. Neighbour-joining phylogeny of the five inf *gregorii* populations showing their occurrence in language group areas according to Harvey [58].** Distan nodes indicates genetic divergence between populations calculated with the D_C method. Arrow indicates mid-po word-forms for boabs associated with each of the five inferred *A*. *gregorii* populations are shown in quotation ma

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Analysis of molecular variance (AMOVA [65]) was used to test whether there was a significant broad scale correlati genetics and language family area. Boab individuals were grouped according to their occurrence in the nPNy famil significance was tested with 999 permutations.

A partial Mantel test of genetic distance vs. language family area with geographic distance as a covariate [66] was whether any statistical significance inferred by the AMOVA was a result of isolation by distance in both language ar variation. Genetic distance was calculated between boab individuals using the D_C method [54], and boab individual to language family areas as described above.

We used a permutation test, implemented in Mesquite [67], to test for statistically significant association between la and genetic identity. The genetic clusters were scored as single, multistate characters. The length of this character phylogenetic tree was calculated under equally-weighted parsimony. We permuted this character 999 times, and ca length on the language phylogenetic tree. We then determined whether the length of the original character was insi distribution based on the randomly permuted character.

Language families and boab word-forms.

To examine the geographic relationship between boab word-forms and language families, the numbers of boab wo of the ***nPNy*** language families were examined to identify languages with higher and lower numbers of boab word-f greater diversity of word-forms for *A*. *gregorii* within language family areas may suggest long-term presence of, and boab populations. Conversely, lower diversity of word-forms for the tree could be either due to recent rapid expansi family area, or to a more recent interaction of those populations with boabs.

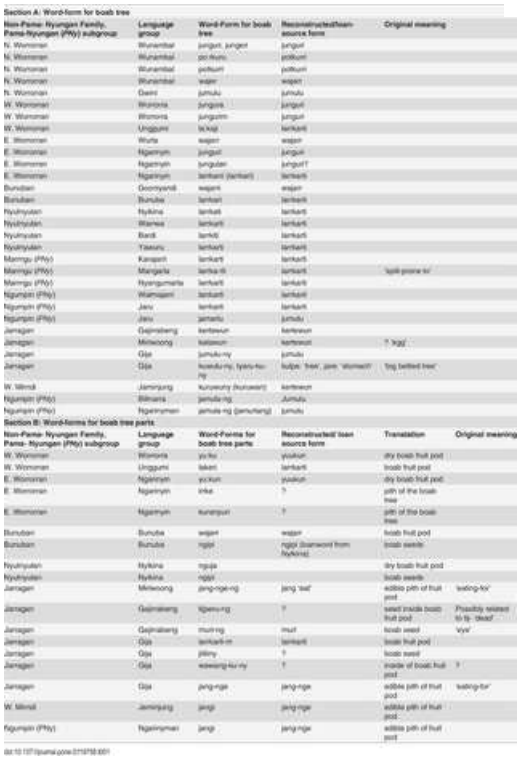

Table 1. Word-forms for *Adansonia gregorii* in the Kimberley region.
doi:10.1371/journal.pone.0119758.t001

Data on boab word-forms and related terminology were drawn from both published and unpublished sources (S2 D left-hand columns identify the non-Pama-Nyungan language family and Pama-Nyungan (*PNy*) sub-groups, and the language groups. The word-forms are represented in a standardized orthography. A hyphen indicates a morpheme separating a stem from a suffix. The subsequent columns list the reconstructed or loan-source form and the probab meaning of the reconstructed source form. Section A lists word-forms for the boab tree; Section B lists word-forms tree-parts.

Boab word-forms and genetic population phylogeny.

If humans have played a major role in dispersing boabs over the Kimberley, then we might expect congruence betw loanwords and dispersal of genotypes. Gene flow between *A*. *gregorii* populations has previously been examined b coalescent analysis, using IMa2 [40]. That analysis yielded estimates of the relative migration rates in two major dir between western and eastern populations and between coastal and inland populations [40]. These directional patte were compared with the directional movement of boab word-forms, especially loanwords, using the comparative me trace their original source and examine patterns of geographic congruence. The reconstructed loan source forms fo in Table 1 were used to identify five words which showed directional movement of borrowing between the language Kimberley region.

Results

Phylogeny of *A*. *gregorii* populations

Phylogenetic analysis generated an unrooted tree for the five inferred populations with bootstrap support values gre for both internal branches (Fig. 2B). Midpoint rooting suggests that the WK and NWC populations are sisters, as ar NEC populations, with the deepest divergence separating the NC population from the other four. However, since th the node, this conclusion should be treated with caution.

Boab populations and language family areas

The association of the five *A*. *gregorii* populations on the language phylogenetic tree (Fig. 2A) and vice-versa, of la with boab population phylogeny (Fig. 2B), did not reveal strict geographic congruence. Statistical analyses showed variance between boab individuals from different ***nPNy*** family areas was low but statistically significant (AMOVA, 3 genetic variation, $P = 0.001$). A partial Mantel test of genetic distance vs. language family area with geographic dist covariate was not significant ($R_{xy} = 0.00728$; $P = 0.285$), indicating that the statistical significance of the AMOVA co spatial autocorrelation in both languages and genetic variation. However, it is noteworthy that there seems to be a sharp distinction between the EK and NEC genetic clusters, and this break coincides with the distinction between th Worrorran language families.

The mapping of genetic population assignments onto the language tree required 4 steps for the original, unpermute the permuted characters required from 5 to 10 steps, with a mean of 8.55. With 999 permutations, this implies a p-v indicating a strongly non-random pattern of association between the language tree and the genetic clusters. Becau was not included as a covariate, we cannot rule out the possibility that this association is driven by geography rathe relationship between boab genetics and human language variation.

Language family areas and *A. gregorii* word-forms

The greatest diversity of word-forms for *A*. *gregorii* is found in the northern coastal areas encompassing the Worror family, followed by those in the Jarragan family (Table 1 and Fig. 2A). Each has one dominant word for the tree spe borrowed from elsewhere. Worrorran has the term *junguri*, and Jarragan has *jumulu*. Both terms are reconstructabl for boab in these language families. In addition to these proto-words and their descendant forms, the language fam inherited word-forms for boabs. Worrorran (Northern) has the forms *potkurri* and *wajarr* in the Wunambal language; is restricted to this specific language, while the latter is also used in Wurla (Eastern Worrorran). *Wajarr* has either b into the Bunuban family or from it: evidence is equivocal at this stage. Forms of the Jarragan proto-word *jumulu* hav borrowed into northern Worrorran and into the ***PNy*** Ngumpin subgroup. Jarragan also has the term *kertewun* that h borrowed further east into the ***nPNy*** Mirndi language family.

Of particular interest is the boab word-form *larrkarti*, which is from a language subgroup associated with the desert the main bioregions of *A*. *gregorii* distribution. Analyzability of this word into two morphemes (*larr*-split; *karti*-side) su comes from the Karajarri (and/or the closely related and neighbouring Mangarla) languages of the ***PNy*** Marrngu su southwest periphery of the Kimberley and is of relatively recent origin [53]. While both the elements *larr* 'split length suffix –*karti* 'towards; side' do occur in other languages in the region separately and with somewhat different meani coincidence with Karajarri and Mangarla languages is a strong indication that this is the origin of the new coined ter As a whole, *larrkarti* means 'split side', which could be an allusion to the hollow trunks of old trees or the dehiscent boab fruit pod, or more likely to the manner in which the shelled fruit splits into longitudinal segments. The coining c well have come about when the Marrngu speaking people moved from the desert into the west Kimberley areas wh have encountered these unfamiliar trees in the landscape. This Marrngu word for boab has been borrowed and inc the vocabularies of some of the ***nPNy*** Worrorran (Western and Eastern) – Bunuban – Nyulnyulan language families Jarragan language alongside other inherited word-forms. *Larrkarti* has also been borrowed into the ***PNy*** Ngumpin la subgroups from desert areas southeast of the Kimberley.

Boab word-forms and genetic population phylogeny

Fig. 2B illustrates the overlap between *A*. *gregorii* words-forms and population phylogeny. The NC population, whic sister to the remaining populations, has the inherited Worrorran boab word-forms *junguri* and *potkurri*, and possibly NWC population has the inherited form *junguri*. The WK population, which clusters with NWC and is distributed acr ***nPNy*** language family areas has three words, *junguri*, *wajarr*, and *larrkarti*. The NEC population has *wajarr*, *jungula* cognate of *junguri*) and the Jarragan loanword *jumulu*. The EK population, which occurs across the Jarragan and M has the word-forms *jumulu* and *kertewun*. Each pair of genetic clusters shares at least one boab word-form sugges word exchange.

Gene flow and diffusion of boab loanwords

Statistically significant gene flow was recorded across all boab populations in the Kimberley [40]. Migration rates we grouping the populations across two axes: West (WK, NWC) ↔ East (NC, NEC, EK); and Coast (NWC, NC, NEC) EK). The West→East migration rate was 0.47 individuals/ year and the East→West rate was 0.11. The Coast→Inla rate was 0.74, and Inland→Coast was 0.50 [40].

We compared these gene flow patterns with inferred loanword diffusion patterns (Fig. 3). The linguistic analysis of b diffusion is consistent with the existence of an East-West biogeographic divide [36–39, 40]: *jumulu* and *kertewun* ha further to the east, but not into west Kimberley, whereas the word *junguri* remains in the northwest and has not diffu Kimberley. *Larrkarti* has diffused widely from its inferred source in the southwest into western and central Kimberley not further into northern Worrorran languages.

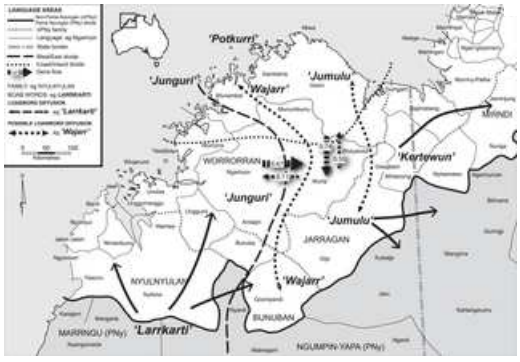

Fig 3. Gene flow between *A. gregorii* populations and boab loanword diffusion across the Kimberley region.
Approximate locations of inferred East-West and Coast-Inland biogeographic divides are represented by dotted l

flow between East-West and Coast-Inland is calculated using IMa2 is in units of individuals/year, and shown with block arrows. Unbroken arrows show the direction of borrowing of boab loanwords among the Kimberley langua arrows show possible directions of loanword movements.
doi:10.1371/journal.pone.0119758.g003

If human-mediated dispersal were responsible for the East ↔West and Coast ↔ Inland dispersal, we might expect corresponding loanword diffusion along these axes. Furthermore, since there is evidence of much more west-to-eas than east-to-west gene flow across the inferred East-West divide, we might expect more west-to-east diffusion of lo the reverse. These directional patterns accord well with the diffusion of boab loanwords shown in Fig. 3. *Larrkarti* a have diffused West→East, but there are no cases of East→West boab loanword diffusion. Thus, the direction and r migration of *A*. *gregorii* gene flow show correspondence with the inferred diffusion of boab loanwords.

Discussion

Our study supports the hypothesis that human-mediated dispersal has played a role in shaping the geographical di *gregorii*. The limited morphological and genetic divergence of the *Adansonia* genus in northwest Australia, despite t biogeographic barriers, can be attributed to high gene flow within *A*. *gregorii* [40]. Given the lack of other obvious se agents, the lack of evidence of barriers to gene flow is most easily explained by a long history of humans moving bo Concordance between gene flow and loanword diffusion further supports the hypothesis of human-mediated disper *gregorii*. Loanword movements across all boab populations provide an indication of patterns of interaction between families and ***PNy*** subgroups that would have influenced the geographic distribution of *A*. *gregorii* in the Kimberley r

Additional evidence of anthropogenic agency in facilitating boab gene flow comes from archaeological excavations Gap Shelter located in the Napier ranges of the Kimberley, which falls within the Bunuba language area [48,49]. Litl macrobotanical remains from this rockshelter site showed continuity of human occupation extending over 40 ka into Pleistocene. Carbon dates recorded boab pod fragments at 39 ka, 20 ka, 18 ka and 15 ka [48,49], with substantial deposition from 3 ka onwards and peaking at around 650 years ago [49]. Old boab trees have been found near abo in western Kimberley, providing further evidence of long-term human consumption of the fruit [48]. Prehistoric rock a northern Kimberley also shows possible depictions of the tree, indicating its cultural significance to ancient human g have occupied this region [28].

Based on the above evidence, we postulate that recent boab evolution and geographic distribution have been shap through ancient human agency. The phylogenetic tree of boab populations and predominant direction of gene flow t that the source populations for *A*. *gregorii* dispersal were most likely in the extreme northwest Kimberley, potentially with the inferred NC population area. The range of this source population is likely to have extended beyond the cur the Last Glacial Maximum (LGM, roughly 20 ka) when sea levels were over 120 m below present-day, and the nort continental shelf was exposed to the maximum extent [68]. The increased land surface exposure of both Sahul and shelfs, lower sea surface temperatures (SST), and altered oceanic currents due to closure of several shallow seas passageways between these continental shelves contributed to a northward shift of the Inter-Tropical Convergence thereby reducing seasonal precipitation levels [69] and creating semi-arid savanna conditions [70] in which ancestra populations would have existed in northwest Australia.

Fig. 4 sketches a possible LGM scenario for this boab population distribution, showing land exposed at 17 ka and a to present-day coastlines. With rainfall as much as 30 to 50% below present day levels [69] and higher levels of aeo activity [71], subtropical desert conditions would have prevailed across much of the exposed continental shelf beyo Kimberley [72–75]. These arid climatic conditions, particularly the low levels of seasonal rainfall, would have limited of *A*. *gregorii*, as the current distribution of the species coincides with areas receiving at least 700 mm of annual sea [76]. Therefore, under drier climatic conditions during the LGM due to the northward shift of the ITCZ [69], it is likely populations would have been limited to the extreme northern coast of present-day Kimberley and the exposed cont

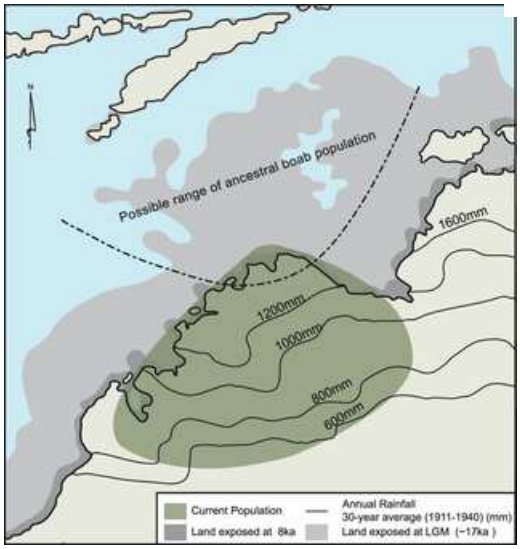

Fig 4. Sketch of LGM scenario showing land exposed at 17 ka and at 8 ka in relation to present-day coastlines, based on Coller [
The possible extent of ancestral boab population distribution on the exposed continental shelf is shown by a das
current boab distribution shown in light grey. Rainfall isohyets (mm) are based on 30-year annual average rainfa
(1911–1940) estimates obtained from the Australian Bureau of Meteorology [88].
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Subsequent sea-level rise and restoration of monsoonal activity during the post-glacial period and the Pleistocene-
transition between 17 and 6 ka flooded the Sahul shelf and established the present-day coastlines of northern Aust
The flooding of the continental shelf beyond the present-day Kimberley coast, along with increased monsoonal rain
Kimberley, would have altered the distribution of ancestral *A*. *gregorii* populations and possibly created a genetic bo
which current populations would have expanded [40]. We propose that ancient human groups that lived on the coas
previously exposed shelf during the Late Pleistocene would have retreated from inundated areas and carried boab
as they migrated further south and east.

Late Pleistocene records of boab remnants at the Carpenter's Gap archaeological site [48,49] may represent spora
human settlers from the north [77]. The site record of the presence of shells and beads from the Early Holocene su
movement of high value goods from the coast [78]. In common with other Australian archaeological sites [79], evide
occupation at Carpenter's Gap increases sharply from mid- to late Holocene, perhaps reflecting a demographic exp
southern Kimberley [79]. This population increase, combined with other factors such as climatic and vegetation cha
growth in local boab populations, and more frequent use of the site for cultural ceremonies and exchanges [77] cou
increase in boab pod remnants along with other food plants and seeds from about 3000 to 650 years ago [48].

The increased mobility of Aboriginal groups in the southern Kimberley during the Late Holocene is likely to have be
greater climate variability in northern Australia. In contrast to the Early Holocene, the Late Holocene (~1000 BCE –
in the Australian Monsoon Tropics was marked by periods of increased seasonality and aridity [80–82]. These conc
contributed to increased mobility of Aboriginal groups between different parts of the Kimberley and would have con
A. *gregorii* gene flow through fruit and seed dispersal, accompanied by diffusion of associated word-forms.

The linguistic data provides additional indication of patterns of migration and social interaction that could have contr
spread of *A*. *gregorii* (Table 1 and Fig. 3). The periods of aridity during the Late Holocene may have affected the su
desert-based Marrngu (***PNy*** subgroup) speakers and led to their migration into southern and western Kimberley. Th
larrkarti was probably coined by Marrngu speakers during this period when they would have encountered the boab
Kimberley landscape. At the same time, the mobility and cultural interactions of these ***PNy*** groups with neighbourin
language groups such as Nyikina and Bunuba would have increased. Evidence that the diffusion of the loanword *la*
relatively recent nature is demonstrated in the way it has been incorporated into other languages, generally in an u
[61]. The Gija language (southern Jarragan) has retained its inherited word *jumulu* for the tree and adopted *larrkart*
perhaps indicating the salience and portability of the edible seed pod in the more recent borrowing. Likewise, the Ja
(***PNy*** Ngumpin subgroup) has no inherited words for boab and uses both *jamula* (modified from Gija) and *larrkarti* f
Other examples of recent boab expansion and loanword diffusion further east can be found in the Ngarinyman lang
in the Northern Territory, where the words *jang-nge* (borrowed from Miriwoong, meaning 'for eating') and *jumulu* (bo
Gija) are used for the fruit or its edible pith, and the tree respectively.

The possible climatic influences on human migration and boab loanword movement in the Kimberley echoes some
Bostoen et al.'s [6] description of climate-induced dynamics and Bantu expansion in Africa. Although there is no an
evidence of a large-scale expansion of a single linguistic group into the Kimberley, the ***PNy*** Marrngu term *larrkarti* a
pre-existing ***nPNy*** language words such as *wajarr*, *jumulu*, and *kertewun* moved across the Kimberley in patterns c

with multi-directional boab gene flow as shown in our study.

The high gene flow in *A*. *gregorii* appears similar to the case of *A*. *digitata* in Africa, where human agency has been dispersal of the species [19,51,52]. The boab loanword movements in the Kimberley may be compared with Blench the spread of Bantu words for *A*. *digitata*. He notes that the genetic diversity of baobabs in the ecological zones of W the diversity of vernacular names for the tree in African languages suggests considerable antiquity as well as signifi movement along trade routes and exchanges of associated ideas and terminology. However, despite the diversity o names, he points out that two competing Bantu roots, #*mbuyu* and #*muramba*, and variations of these, are found in languages of southern and eastern Africa. The Bantu expansion from the tropical forest areas of West Africa is said from around the middle of the first millennium BC (~ 2500 BP onwards) and reached southern Africa by about 500 C Blench argues that the Bantu would not have been familiar with the baobab because it does not grow in the tropical Cameroon, Gabon and Congo where this proto-language group are thought to have originated. They would have en tree as they expanded eastwards and emerged into the savanna, and developed new terms by either borrowing fro hunter-gatherer groups or comparing it with some other tree species they already knew. The loan or variations of ba *mbuyu* and *muramba* in the Bantu languages of eastern and southern Africa would thus indicate the movement of B areas [4]. The lower levels of genetic diversity of *A*. *digitata* in eastern and southern Africa detected by Leong Pock may likely be due to the Bantu expansion over this 3000 year period and their contribution to high levels of gene flo across these regions.

Conclusion

Our study demonstrates that the limited intraspecific divergence within *A*. *gregorii* in Australia is most likely due to h mediated by human agency, similar to that inferred for *A*. *digitata* in continental Africa [27, 51], combined with shifts habitat and a weak bottleneck following the end of the LGM [40]. Human use of *Adansonia* over many thousands of continents would have contributed to gene flow over long distances and across biogeographical barriers. In contras the divergence of *Adansonia* into six species in Madagascar was possible in part because of the lack of humans un However, this hypothesis can only be tested by further investigation of the ecological, physiological and biogeograp contributing to speciation within the *Adansonia* clade from Madagascar.

This study contributes new evidence for the role of ancient humans in influencing the evolution and distribution of n plant species in Australia. Australia has long been viewed as a continent of hunter-gatherers [84] where prehistoric populations prior to European colonisation played minimal roles in selecting and dispersing useful plants [23,24]. H recent studies have challenged this assumption by providing evidence for the role of ancient Aboriginal groups in th food plants across the continent [77,85,86]. These include bananas (*Musa* spp.), taro (*Colocasia esculenta*) and so (*Dioscorea* spp.) in northern Australia [23], *Livistona* palms in Central Australia [85], and yam daisy (*Microseris sca* southeastern Australia [86]. Our findings add new insights regarding the role of ancient human agency in influencin and distribution of the boab, an important non-cultivated food plant species that has shaped the long-term landscap environmental history of northwest Australia.

Supporting Information

S1 Dataset. Genetic data from six nuclear microsatellite loci of 220 *A*. *gregorii* individuals.

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(XLS)

S2 Dataset. Terms for boab in Aboriginal languages of the Kimberley region.

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Author Contributions

Conceived and designed the experiments: KLB RF DJM. Performed the experiments: KLB RF. Analyzed the data: K TS SS. Contributed reagents/materials/analysis tools: KLB HR. Wrote the paper: HR KLB DAB. Conceived the ove project: HR DJM CAK. Analysed the genetic data: KLB RF DAB. Contributed collection of boab terms in Aboriginal Kimberley region and analysed the linguistic data: PM TS SS.

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